Subterranean Biology 49: 97–116 (2024)
doi: 10.3897/subtbiol.49.130692
https://subtbiol.pensoft.net

RESEARCH ARTICLE

A peer-reviewed open-access journal
Subterranean Biology
Published by The International Society for Subterranean Biology

Lost & Found - Rediscovery of H. Hauffen's *Carychium* material in the Dominik Bilimek Collection, BOKU University, including a contemporary assessment within the genus *Zospeum* (Gastropoda, Ellobioidea, Carychiinae)

Petra Lukeneder[1,2], Franz Ottner[2], Mathias Harzhauser[3], Viola Winkler[4], Brian Metscher[5], Bernhard Ruthensteiner[6], Adrienne Jochum[7,8]

1 *Doctoral School of Ecology and Evolution, University of Vienna, Djerassiplatz 1, 1030 Vienna, Austria* **2** *Institute of Applied Geology, BOKU University, Peter Jordan Strasse 82, 1190 Vienna, Austria* **3** *Geological-Paleontological Department, Natural History Museum Vienna, Burgring 7, 1010 Vienna, Austria* **4** *Central Research Laboratories, Natural History Museum Vienna, Burgring 7, 1010 Vienna, Austria* **5** *Department of Evolutionary Biology, University of Vienna, Djerassiplatz 1, 1030 Vienna, Austria* **6** *Zoologische Staatssammlung München (ZSM), Münchhausenstraße 21, 81247 München, Germany* **7** *Natural History Museum Bern, Bernastrasse 15, 3005 Bern, Switzerland* **8** *Senckenberg Research Institute and Natural History Museum, Senckenberganlage 25, 60325 Frankfurt am Main, Germany*

Corresponding author: Petra Lukeneder (a0501032@unet.univie.ac.at)

Academic editor: Alexander Weigand | Received 27 June 2024 | Accepted 19 August 2024 | Published 3 September 2024

https://zoobank.org/F50A35EF-B724-48DE-9437-5E2BAB9F7873

Citation: Lukeneder P, Ottner F, Harzhauser M, Winkler V, Metscher B, Ruthensteiner B, Jochum A (2024) Lost & Found - Rediscovery of H. Hauffen's *Carychium* material in the Dominik Bilimek Collection, BOKU University, including a contemporary assessment within the genus *Zospeum* (Gastropoda, Ellobioidea, Carychiinae). Subterranean Biology 49: 97–116. https://doi.org/10.3897/subtbiol.49.130692

Abstract

The syntypes of *Carychium reticulatum* Hauffen, 1856 and *Carychium bidentatum* Hauffen, 1856, thought to be lost to science, have been rediscovered in a recent inventory of the shell collection of Domink Bilimek (1813–1884) at the University of Natural Resources and Life Sciences in Vienna, Austria (BOKU). In this work, we present (1) the historical context of the Dominik Bilimek and Heinrich (also: Henrik) Hauffen collections and (2) provide a contemporary image dataset of Hauffen's original material while considering today's taxonomic understanding of the genus *Zospeum*. We clarify the taxonomic status of the syntypes by using light microscopy, Scanning Electron Microcopy (SEM) and 3D X-ray Micro-CT data in conjunction with Hauffen's original illustrations and compare them to contemporary investigations of their closest congeners. Analysis of *Zospeum reticulatum* (Hauffen, 1856) is supported by historical

Copyright *Petra Lukeneder et al.* This is an open access article distributed under the terms of the Creative Commons Attribution License (CC BY 4.0), which permits unrestricted use, distribution, and reproduction in any medium, provided the original author and source are credited.

documentation from Heinrich Hauffen's original annotations and Bilimek's diary entries, as well as from individual collection labels in Hauffen's own script (verified by archive material from the Archive of the National Museum of Slovenia, NMS). Hauffen's descriptions are based on apertural morphology and shell microstructure. Our re-investigation of *Zospeum reticulatum* provides corroborating evidence supporting its assignment to *Zospeum spelaeum* (Rossmaessler, 1839) while that of *Carychium bidentatum* corroborates its status as junior synonym of *Zospeum costatum* (Freyer, 1855).

Keywords
Cave snails, history of sciences, natural history collections, type specimens

Introduction

The importance of original type specimens is unquestionable for taxonomic evaluations and for upholding the international standards of reference that provide objectivity in zoological nomenclature (ICZN 1999). There are many incidences where original specimens were not preserved, became lost (Inäbnit et al. 2019), or got destroyed in the ravages of war (Janssen 2006). However, sometimes valuable material reappears serendipitously during inventories of other collections (Albano and De Mattia 2010; Salvador et al. 2023). We present a case in point, whereby the syntypes of *Carychium reticulatum* Hauffen, 1856 and *Carychium bidentatum* Hauffen, 1856, of the troglobitic genus, *Zospeum* Bourguignat, 1856, from Heinrich Hauffen's original collection, considered lost, reappeared in the natural science collection of Dominik Bilimek, housed at the University of Natural Resources and Life Sciences in Vienna, Austria (BOKU). In this paper, we present the historical context of the Bilimek and Hauffen collections (for biographic information see also Lukeneder et al. 2023) and provide a contemporary image dataset of Hauffen's original material considering today's taxonomic understanding of the genus *Zospeum*. We assess the species using light microscopy, SEM and X-ray Microcomputer-Tomography (X-ray Micro-CT) data. Current geographical information regarding older cave names is provided.

Zospeum reticulatum is considered a junior synonym of *Zospeum spelaeum* (Rossmaessler, 1838) in the most recent work of Inäbnit et al. (2019). Historically, *Zospeum spelaeum* is a much-debated species showing a wide spectrum in representation of shell characters, from smooth shells to ribbed shells to those that are highly reticulated and bidentate or tridentate (Frauenfeld 1856; Hauffen 1856a). Although Hauffen (1856b) found his shells very similar to those of *C. schmidtii* (Frauenfeld, 1854), he and Von Frauenfeld (1856) debated over the taxonomic significance of the number and position of denticles and the density of reticulate microstructure on the teleoconch as unique, diagnostic characters. Meanwhile, contemporary methods of analysis have enabled major access into the shells of these microscopic snails, not possible in 1856. These have revealed new image data providing evidence of the taxonomic significance of signatory structures such as the shape and form of the columellar apparatus, the form of the lamella and the alignment and configuration of the umbilical zone (Inäbnit et al. 2019; Jochum et al. 2024).

In this present work, and in the absence of supporting DNA sequence data from these populations, we delve into Hauffen's and Frauenfeld's morphological quandary by re-investigating this recovered material via new image data while cross checking the potential taxonomic significance of the initial species designation (i.e., *C. reticulatum* versus Frauenfeld's *C. schmidtii* and Freyer's *Z. costatum*). Consequences ultimately would affect species status and taxonomic assignment within *Zospeum*.

Materials and methods

Study material

All shells studied herein stem from the collection of the Institute of Applied Geology at the University of Natural Resources and Life Sciences (BOKU). All specimens include the original collection labels, including information on the determination and the respective author, the site locality and sometimes also the collector. Details about Bilimek's natural science collection are documented in Hopfensperger et al. (2021) and Lukeneder et al. (2023). Heinrich Hauffen catalogued most specimens/groups of specimens with a distinct combination of numbers, which were written on the corresponding label, whereas each combination is unique in his collection (top number corresponds to the species number, base number most probably to the locality number (Fig. 5N). Some labels also include markings with a prominent cross. All inventoried specimens were examined in detail and compared to the material described and illustrated by Hauffen (1856a, b). Localities correspond to Hauffen's documentation. One specimen of *Carychium reticulatum* var. *bidentatum* Hauffen is preserved from Glaven verh. Bibliographic and biographic accounts provide historical context.

Institutional abbreviations

BOKU Institute of Applied Geology, BOKU University (Vienna, Austria);
IPUW Department of Palaeontology, University of Vienna (Vienna, Austria)
MCSNTS Museum of Natural History of Trieste (Trieste, Italy);
NHMW Natural History Museum Vienna (Vienna, Austria);
PMS Slovenian Museum of Natural History (Ljubljana, Slovenia).

Image acquisition

Digital imaging and image processing

The individual shells were imaged using a digital Keyence 3D Digital VHX-600 microscope at the IPUW (Micro photography). Additionally, special features were photographed with a Discovery.V20 Stereo Zeiss microscope and processed with the software AxioVision SE64 Rel. 4.9 imaging system at the NHMW (Microphotography). Col-

lection labels were imaged with a Nikon D 5200 SLR, lens Micro SX SWM MICRO 1:1 Ø52 Nikon AF-S, Digital Camera, combined with the graphic tool (freeware) digiCamControl Version V.2.1.2.0 (Macro photography).

Measurements

Shell measurements, including shell height (sh), shell width (sw), aperture height (ah), aperture width (aw), height of last whorl (hlw) and spire angle (SA), were directly made on the Micro-CT images using dimension tools of the software Corel Draw 2017 (Corel Corporation, Ottawa, Ontario, Canada).

X-Ray Micro-Computer tomography (Micro-CT) and image processing

Three selected specimens were imaged intact in the Theoretical Biology Unit of the University of Vienna Evolutionary Biology Department, University of Vienna, Austria, with a Bruker SkyScan 1272 micro-CT system. The tungsten X-ray source was set at 60 kV and 10 W nominal output, with a 0.25 mm Al beam filter. Projection images were acquired at 0.10° steps and 2.0 μm pixel size. Tomographic images were reconstructed using the Bruker NRecon software, resulting in reconstructed voxel sizes of 2.0 or 3.0 μm (isotropic).

The same samples were also imaged using Micro-CT imaging (YXLON FF35 CT, FXE Transmission Beam, Perkin Elmer Y.Panel 4343 CT) at the NHMW. The scanning parameters were set to 110 kV and 400 μA, while using a 0.2 mm copper filter. A total of 3600 projections images were taken with an exposure time of 2 s each, which volume data sets with isometric voxel sizes of 1.8 μm. Further 3D graphical procedures were performed using Amira version 6.4 software (Thermo Fischer Scientific, Electron Microscopy Solutions, Hillsboro, Oregon, USA) with manual segmentation to separate external and internal shell structures. Final visualization was conducted using the Volume Rendering module.

Scanning electron microscopy (SEM)

The microstructure of three selected gastropod shells was imaged using the FEI Inspect S50 at low-vacuum mode at the laboratories of the IPUW. Images were generated using a backscattered electron detector (BSED). Additional photos were taken using the Large Field-Detector (LFD).

Historical context

The collector, Dominik Bilimek (1813–1884), was a Cistercian monk, naturalist and member of the Austrian Volunteer Corps in Mexico ("Freiwilligenkorps") (1865–1867) (Roth 1965, 2016, 2017) (Fig. 1A), who cultured multiple interests, focusing mostly on entomology and botany. He pioneered biospeleology (in 1846) along with

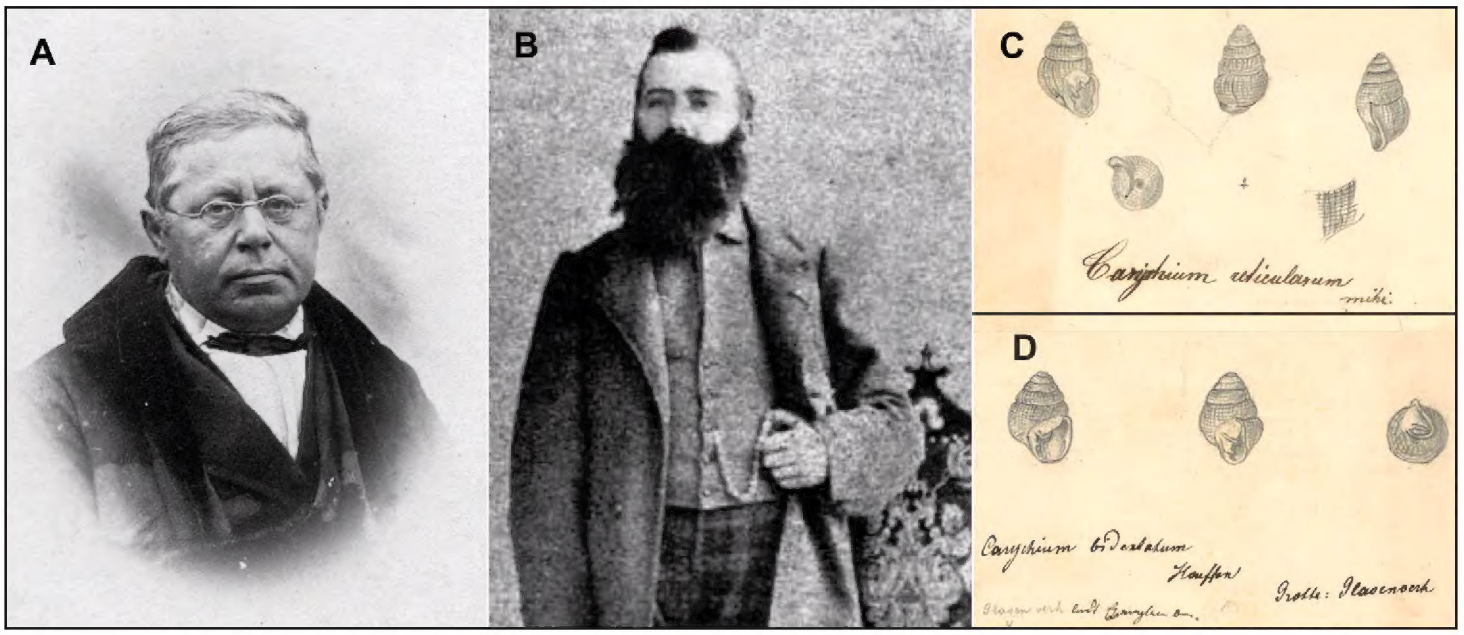

Figure 1. Two collaborating naturalists of the 19th century **A** naturalist and collector Dominik Bilimek (portrait 1864; by courtesy of Fototeca dei Civici Musei di Storia ed Arte Trieste, Italy; inventory no. 4738R) **B** the only preserved portrait of Heinrich Hauffen (Digitalna knjižnica Slovenije, also: Digital Library of Slovenia, reference number 5S74D58Z, Ilustrirani Slovenec) **C** drawing of *Carychium reticulatum* from the H. Hauffen (1856b) manuscript (Archiv NMS, leto 1856, št. 47) **D** drawing of *Carychium bidentatum* from locality Glaven verh; H. Hauffen (1856b) manuscript (Archiv NMS, leto 1856, št. 47).

his contemporaries, including the known 19th century researchers, Adolph Schmidt (1806–1889), Heinrich Freyer (1802–1866) and Heinrich Hauffen. Many of these explorations and contacts are documented in Bilimek's three travel diaries, kept in the archives of the Monastery of Heiligenkreuz (Lower Austria) (Inventory number Rub. 71, fasc. VI, Nr. 10). Bilimek's extensive social networking can additionally be traced throughout his collections, especially on the original collection labels with detailed metadata about collectors and collection dates (Lukeneder et al. 2023). The Bilimek collection also contains material of certain species described by Hauffen - mainly recent snails - including the syntype material of *C. bidentatum* (Hauffen, 1856) and *C. reticulatum* Hauffen, 1856. The corresponding collection labels differ from those of the other labels not only by the handwriting style, but also by the different mode of documentation and the designated boxes containing the associated specimens (see also Lukeneder et al. 2023). Bilimek's collection harbors additional specimens of *C. bidentatum* Hauffen, 1856, now *Zospeum costatum* (Freyer, 1855), and congeners which Hauffen recorded from other Slovenian caves: Douga jama; Kosja jama (better known as: Pri ilavi luzi jark; "Höhle an der Lehmlacke, "Räuberhöhle" in German; see also Wenzel 1992) and Gypsosa jama (near Bischoflack; Hauffen 1858b) (Table 1).

The most remarkable fraction in D. Bilimek's collection of land and freshwater gastropod shells can be assigned to the naturalist, Heinrich Hauffen (1836–1866) (Fig. 1B), an assistant tradesman inspired by the Austro-Hungarian businessman, speleological explorer and naturalist, Ferdinand Joseph Schmidt (1791–1878). Hauffen was especially interested in speleology and zoology and was scientifically tightly affiliated

Table 1. List of specimens including inventory number, cave locality, original Hauffen designated name and number of specimens per locality in the BOKU collection.

Inventory number	locality	taxon	number of specimens
BOKU F3429	Douga jama, Slovenia	*Carychium bidentatum*	5
BOKU F3434	Bidou sturm, Slovenia	*Carychium reticulatum*	12
BOKU F3444	(Grotte hinter) Laak, Slovenia	*Carychium reticulatum*	10
BOKU F3473	Glaven vrh, Slovenia	*Carychium bidentatum*	1
BOKU F3642	Kosja Jama (Kozja Jama), Slovenia	*Carychium bidentatum*	6
BOKU F3643	Gypsosa jama, Slovenia	*Carychium reticulatum*	4

with Heinrich Freyer, zoologist Georg von Frauenfeld (1807–1873) and the naturalist, Dominik Bilimek. Together with Heinrich Freyer, Hauffen pioneered biospeleology, engaging in extensive speleological exploration, investigation, and taxonomic description of cave snails in the region of the former "Krain" (including parts of today's Slovenia and Carinthia, Austria). In an extensive treatise on the genus *Carychium*, Frauenfeld re-investigated zospeid snails (Frauenfeld 1856), including submitted specimens from Heinrich Hauffen from other caves.

Heinrich Hauffen's name occurs in the Bilimek diaries several times. A visit by Bilimek in "Krain" (historical name for the Austro-Hungarian part of Slovenia and Styria (Austria)) (organised by the naturalist Heinrich Freyer) was documented in notes of the first Bilimek travelling diary. He explored the Seeler Grotte (also Željnske jame or Sele'er Grotte) in Unterkrain (today part of Slovenia). This cave is mentioned as the type locality of the coleopterid *Anophthalmus bilimekii* ("Bilimek's Blindlaufkäfer" which Bilimek (Schiner 1854) investigated in 1846 and described in 1847, see also Sturm 1847). On 7 September 1846, the explorers, Bilimek, botanist Stephan L. Endlicher (1804–1849) and another unidentified person visited the nearby cave Križna jama (also Cross Cave, Kreuzberghöhle near Lož/Laas; formerly: Grotte Podlaase) (see also Lukeneder et al. 2023).

From 1865 to 1867, Bilimek and Hauffen both followed Archduke Ferdinand Maximilian Joseph (Archduke Ferdinand Maximilian Joseph Maria from Austria; 1832–1867) and his wife Empress Charlotte (Marie Charlotte Amélie Augustine Victoire Clémentine Léopoldine from Belgium; 1840–1927), as members of the Austrian Volunteer Army Corps to Mexico in May 1865 (Roth 1965). Dominik Bilimek was the 7th museum director and collection custodian at the Natural History Museum in Mexico. Bilimek's and Hauffen's time in Mexico is documented only by few diary entries including a field trip recorded by Hauffen and Bilimek on September 25, 1865, stating, "*on the second mountain behind Quadaloupe*" (Mexico) that they collected eight new plants and two insects. Other entries record November 29, 1865, Bilimek, Hauffen and the Mexican captain, Gonzalez, from the ship Guardia Estable aus Tetela del Oro (see also Roth 1965) collecting insects and cicadas in St. Angel and Petregal (both Mexico) as well as a field trip by Bilimek and Hauffen on December 2, 1865, in Petregal (Mexico) (see also Dominik Bilimek diary no. 2, entry no. 454). A corresponding collection label exists in the Bilimek collection (such as andesitic lava, collected in Mexico, Piedregalle, on 2 December 1865) (Lukeneder et al. 2023).

However, it is not documented, how the Hauffen collection became part of the Bilimek collection. Heinrich Hauffen intended to sell his collection of land and freshwater gastropods, consisting of 10.000 specimens and more than 800 species already in the year 1859 (Frauenfeld 1860). Unfortunately, it is also not documented whether the sale actually took place. Moreover, there are two letters from Dominik Bilimek sent to Emperor Maximilian preserved at the Austrian State Archives (Austrian State Archives signature no. AT-OeStA/HHStA FA MvM 46-2-5), dated 6 April 1866 and 1 May 1866. In one of them, Bilimek requested that the zoologist, Heinrich Hauffen, be dismissed from his position as assistant at the 'future National Museum' in Mexico because he was no longer able to perform his duties due to severe illness (Letter from 1 May 1866. Austrian State Archives signature no. AT-OeStA/HHStA FA MvM 46-2-5). Heinrich Hauffen died in Mexico on 28 June 1866, aged 30. Since they were collaborating, close friends in Mexico, it can be assumed that Bilimek inherited Hauffen's scientific collection after his death.

Data availability

All used data are included within the manuscript and are available upon request from the authors.

Results

The six syntype lots from the Bilimek Collection - catalogued at the BOKU - are listed in chronological order by their collection registration number in Table 1. The specimens are imaged and discussed in more detail below. Information about their synonymy and chresonymy is provided.

Systematic section

Genus *Zospeum* Bourguignat, 1856

***Zospeum spelaeum* (Rossmaessler, 1839)**
Figs 2, 3, 4

Carychium spelaeum Rossmaessler, 1839, Icon., (1) 2 (1/2): 36–37, pl. 49 fig. 661 (shell) [in der Adelsberger Höhle in Krain an Stalaktiten (Postojnska jama, near Postojna)].

Carychium reticulatum Hauffen, 1856, Verh. zool.-bot. Ges. Wien, Abh., 6: 623–624, pl. 7 fig. 4 (shell) [In der Grotte Bidou sturm (Hauffen leg.; Dobruška jama, near Vodice)].

Zospeum spelaeum: twelve junior synonyms are attributed to *Z. spelaeum* (see Inäbnit et al. 2019).

Figure 2. Light microscopic images of Hauffen's specimens of *Carychium reticulatum* var. *bidentatum* Hauffen, 1856 (syn. *Z. spelaeum* Rossmaessler, 1839) BOKU F3434 from the type locality cave, Bidou sturm in Slovenia **A–D** Shell specimen BOKU F3434b in apertural view (**A**), dorsal view (**B**), apical view (**C**), umbilical view (**D**) **E–H** shell specimen BOKU F3434a in apertural view (**E**), dorsal view (**F**), apical view (**G**), umbilical view (**H**) **I–L** Shell specimen BOKU F3434j in apertural view (**I**), dorsal view (**J**), apical view (**K**), umbilical view (**L**). Scale bars: 1 mm.

Material examined. *Carychium reticulatum* Hauffen: imaged syntype BOKU F3434b, other syntypes BOKU F3434a, BOKU F3434j, Cave Bidou sturm [= Dobruška jama], coll. Bilimek ex Hauffen 1856.

Diagnosis (Hauffen original from German). "Distinct vertical and horizontal lines form an entirely complete network pattern unique to this species".

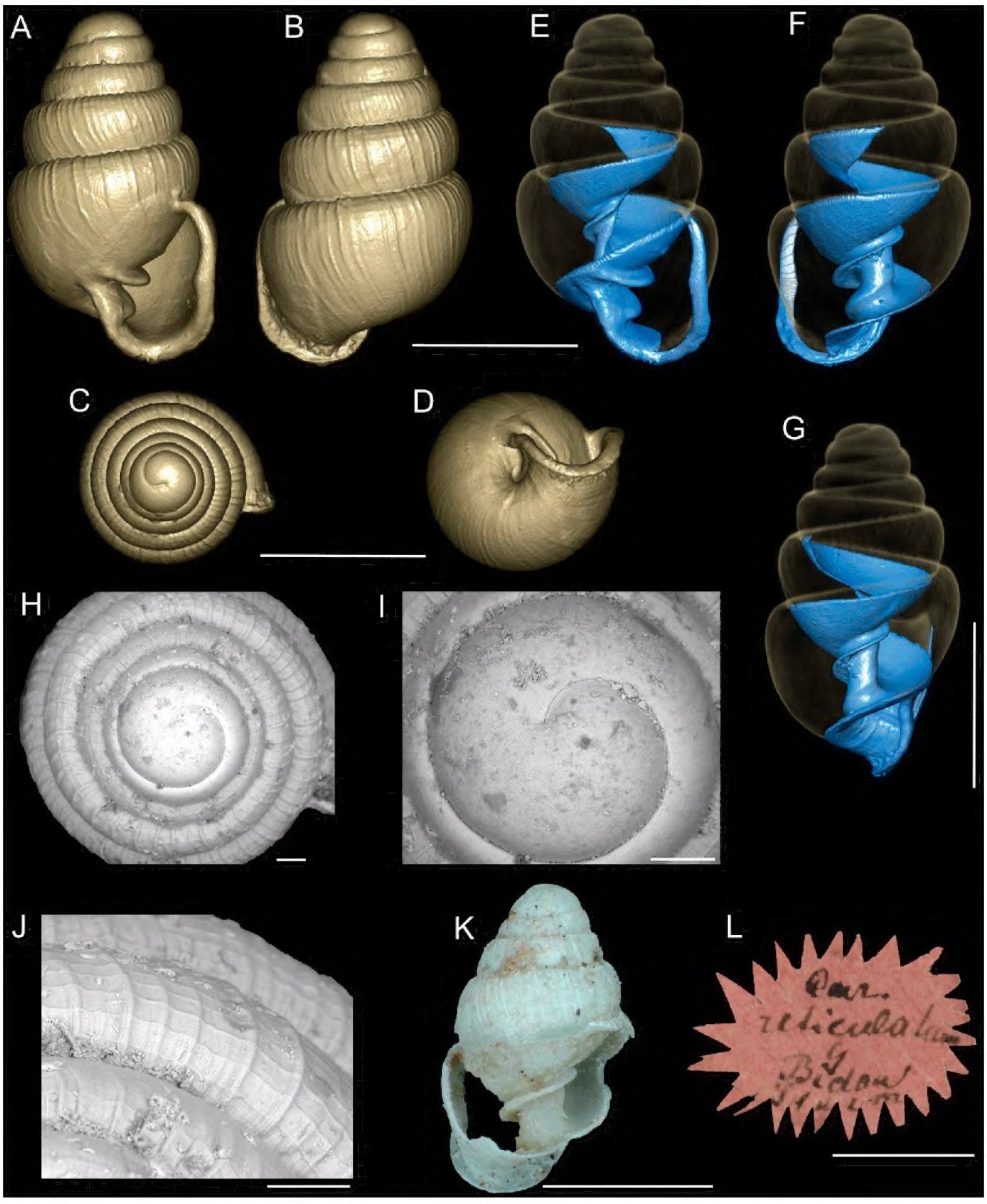

Figure 3. Hauffen's specimens of *Carychium reticulatum* Hauffen, 1856 from the type locality, Bidou sturm in Slovenia. Inventory number BOKU F3434 **A–G** 3D visualizations of Micro-CT data of specimen BOKU F3434b showing the columellar apparatus; apertural view (**A, E**), dorsal view (**B, F**), apical view (**C**), umbilical view (**D**), lateral view (**G**) **H–J** scanning Electron Microscopy images of shell F 3434j (apical view) **I** detail of **H** showing protoconch **J** reticulated sculpture of *Zospeum reticulatum* Hauffen, 1856 **K** broken shell of specimen BOKU F3434d in dorsal view exhibiting collumellar apparatus **L** collection label of BOKU F3434. Scale bars: 1 mm (**A, B, C, D, E, F, G**); 100 μm (**H, I, J**); 1 cm (**L**).

Description (Hauffen original from German). "Shell with 6 whorls, the last is relatively large; suture moderate; shell glassy and transparent; the sculpture is ribbed with the ribs largest by the suture, between these are often smaller ribs which extend to the middle of the whorl, the long ribs begin in most cases at the third whorl and

continue over the cross ribs; near the suture they are closer to each other, in the middle of the whorl [zone of greatest convexity] they are however further apart, these crossed over ribs form a network, hence the name; umbilicus somewhat open at the beginning, however closing rapidly, aperture elongate, peristome rim bent backwards, lipped, dented in on the right side; columella somewhat swollen, on which a small denticle is in the middle, which lies deeper inside the aperture, on the inner parietal side are two denticles, the one nearest the columella is the larger and begins closest to the opening, it is next to the smaller one, which lies deeper in the aperture, bending to the right, this smaller interior denticle is visible in some shells and barely visible in others, the parietal shield shows tiny pitting. Height 2.0–2.2 mm. Width 1.5 mm."

Measurements. (BOKU F3434b from Bidou sturm): sh = 2.14 mm; sw = 1.26 mm; ah = 1.01 mm; aw = 0.84 mm; hlw = 1.43 mm; SA = 58.55 deg.

BOKU F3429 from Douga jama: sh = 1.96 mm, sw = 1.18 mm; ah = 0.94 mm; aw = 0.78; hlw = 1.29; SA = 59.90 deg.

Distribution (Hauffen *Z. spelaeum*). Caves Bidou sturm (= Dobruška jama) and Douga jama.

Remarks. Hauffen also recorded this species from a cave behind Laak. Re-investigation of his specimens from that cave herein (Fig. 5) revealed that they are not conspecific with *Z. spelaeum* from Bidou sturm (Figs 2, 3) but rather, with the species *Z. costatum* (Freyer, 1855) (see Inäbnit et al. 2019, fig. 5, C1–3).

Enhanced description of *Z. spelaeum* based on integrative taxonomic analyses of Inäbnit et al. (2019) and Micro-CT and SEM Data in this work.

Diagnosis. Shell ca. 1.96 mm, transparent, elongate, or elongate-conical with an auriform and more or less thickened peristome, bearing two to three apertural barriers; columella with a single lamella.

Description. Shell conical, often more slender than other species, translucent when fresh; whorl never well rounded [as, for example, in *Zospeum frauenfeldii* (Freyer, 1855)], usually ovate-conic in form; shell surface usually ribbed, but variable, which has been used to differentiate subspecies in the past (present on the whole whorl as in "*Z. s. costatum*", present on the upper part of the whorl as in (*Z. s. schmidtii* (fig. 4f–n) or completely absent as in (*Z. s. spelaeum*) (fig. 4a–e) (Inäbnit et al. 2019)), but the spectrum of variation within populations is too broad to establish congruence here; aperture taller than wide, the palatal side usually shouldered; the parietal shield well-differentiated from the lip, its shape either convex or straight; parietalis well-developed in the aperture, extending one whorl into the shell; columellaris visible in the aperture, in some cases disappearing within half a whorl into the shell or continuously weakening; a more or less oblique lamella is present above the middle of the short columella; a basal bulge is present just above the umbilicus; angularis in most cases present as a tooth of variable prominence; palatalis usually present. Protoconch covered with pits; interconnected pits on top of the protoconch densely aggregated into rows; pits

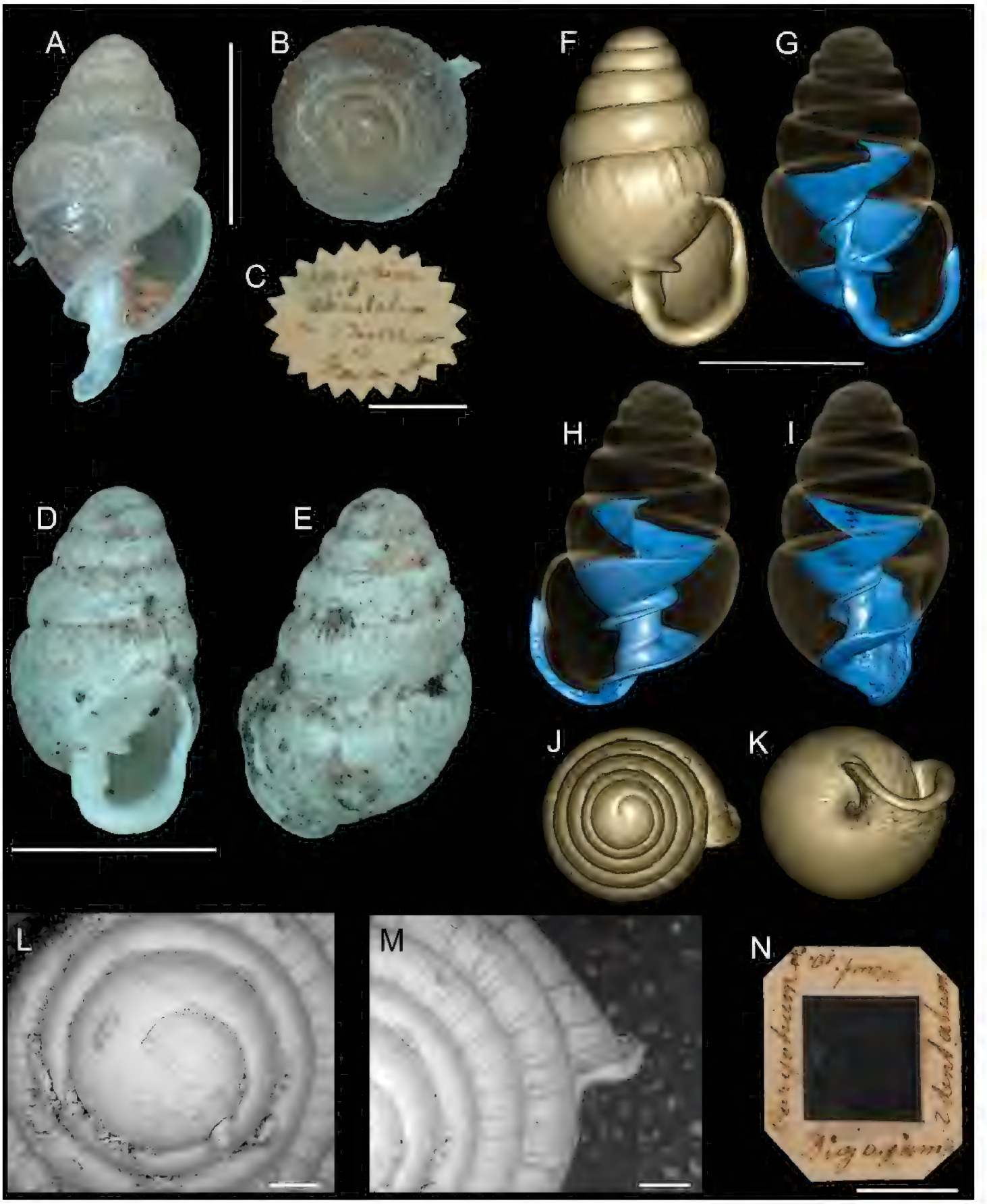

Figure 4. Hauffen's specimens of *Carychium*" *reticulatum* var. *bidentatum* Hauffen, 1856 (syn. *Z. spelaeum* Rossmaessler, 1839) from Glaven verh (Slovenia) and from Douga jama cave (Slovenia) **A, B** light microscopic images of broken shell BOKU F3473a from Glaven verh showing apertural view (**A**), apical view (**B**) **C** collection label of broken shell BOKU F3473a **D–K** specimens of BOKU F3429 from Douga jama (Slovenia) **D, E** light microscopic images of specimen BOKU F3429a showing apertural view (**D**), dorsal view (**E**) **F–K** 3D visualizations of Micro-CT data of specimen BOKU F3429b; apertural view (**F**), apertural view showing columellar apparatus (**G**), dorsal view showing columellar apparatus (**H**), lateral view (**I**), apical view (**J**), umbilical view (**K**) **L, M** scanning Electron Microscopy images of shell of BOKU F3473a from Glaven verh (**L** apical view **M** detail of reticulate microstructure on teleoconch) **N** collection label of BOKU F3429 with notation referring to Douga jama locality. Scale bars: 1 mm (**A, B, D, E, F, G, H, I, J, K**); 100 μm (**L, M**); 1 cm (**C, N**).

on the side of the whorl distributed more randomly. Details of the radula and the *Z. spelaeum* clade within the most recent phylogeny of *Zospeum* are available in Inäbnit et al. (2019).

The *Z. spelaeum* shells herein (BOKU F3434b and BOKU F3429) show a well-formed oblique lamella on a centrally aligned columella, the base of the columella shows a basal, lamella-like bulge in dorsal and aperture facing right views (Figs 3F–G, 4H), forming the more or less pronounced columellaris, which ends deep in the shell and is visible behind the peristome on the columellar side (Figs 3A, E, 4D, F); the robust and well-developed parietalis extends one whorl into the shell, tightly exiting the columellar side of the peristome far up on the parietal shield, ending either before or up to its outermost edge (Fig. 3A, D); umbilical depression deep; columellar side of peristome arches over and oblique to umbilical depression on ventral side (Figs 3D, 4K), alignment of last ¼ whorl not compact. Central part of protoconch partially covered with interconnecting pits and singular pits aggregated in rows (Figs 3I, 4L); onset of ribbing begins at suture of second or third whorl and with increased reticulation of the third whorl some distance from the suture. More or less enhanced reticulation begins at the fourth whorl (Fig. 3H).

Considering the 148 specimens investigated in Inäbnit et al. (2019) and those of this study, *Zospeum spelaeum* differs from *Z. costatum* by a less expanded upper section of the palatal side of the aperture; from *Z. lamellatum* Bole, 1974 by its greatly reduced external ribbing and number and size of lamellae and apertural barriers; from *Z. lautum* (Frauenfeld, 1854) by its usually more slender shell, the presence of ribs, and its bearing a simple inclined lamella versus the more elaborate 3-tiered lamellar configuration in *Z. lautum*; from *Z. trebicianum* Stossich, 1899 by its larger size.

Distribution. *Z. spelaeum* is known from the region of Ljubljana, Slovenia westwards to the Brenta River in Italy, the region of Trieste, Italy, the island of Cres, and eastwards where the Sava River enters the Julian Alps and from the Vrlovka cave in the northeastern part of Croatia (see also De Mattia 2003).

Zospeum costatum (Freyer, 1855)

Fig. 5

Carychium costatum Freyer, 1855, Sitzungsber. mathem.- naturw. Cl. kais. Akad. Wiss. Wien, 15 (1): 20, pl. [1] fig. 5a–c (shell) [Von Herrn Ferd. Schmidt in der Grotte bei Goričane unweit des fürstbischöflichen Schlosses Görtschach entdeckt (Babja Luknia, near Goričane)].

Carychium bidentatum Hauffen, 1856, Verh. zool.-bot. Ges. Wien, Abh., 6: 701, pl. 7 fig. 5 (shell) [„in der Grotte am Glaven vrh“ (Hauffen leg., 17 exx.)] (Hauffen 1856b).

Material examined. *Carychium bidentatum* Hauffen: imaged syntypes BOKU F3444a (Grotte hinter Laak), BOKU 3473a (Glaven vrh); other syntypes BOKU F3444b, BOKU F3444d, Cave behind Laak, coll. Bilimek ex Hauffen 1856.

Diagnosis (Freyer, original from German). Vertically ribbed, bidentate carychid.

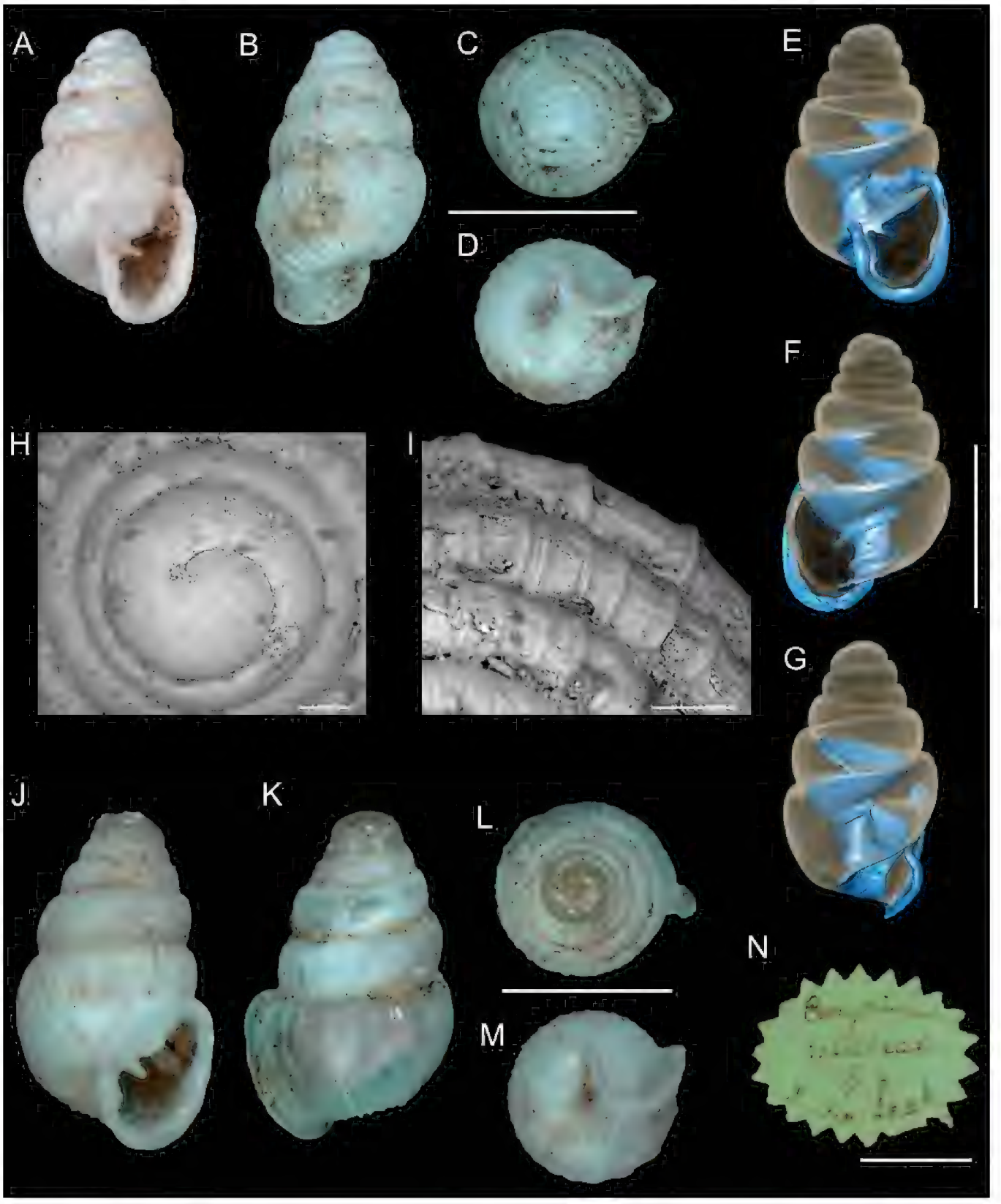

Figure 5. Hauffen's specimens of *Zospeum costatum* (Freyer, 1855) from Laak in Slovenia. Inventory number BOKU F3444 **A–D** shell specimen F3444b in apertural view (**A**), dorsal view (**B**), apical view (**C**), umbilical view (**D**) **E–G** 3D visualizations of Micro-CT data of shell specimen BOKU F3444a showing the columellar apparatus. Apertural view (**E**), dorsal view (**F**), lateral view (**G**) **H, I** scanning Electron Microscopy images of shell specimen BOKU F3444b (apical view) **J–M** shell specimen F3444d in apertural view (**J**), dorsal view (**K**), apical view (**L**), umbilical view (**M**) **N** collection label of BOKU F3444 with characteristic handwriting of Heinrich Hauffen. Scale bars: 1 mm (**A, B, C, D, E, F, G, J, K, L, M**); 100 µm (**H, I**); 1 cm (**N**).

Description (Freyer, original from German). Shell white, spired, overlayed with strongly pronounced vertical ribs. Those of the first four graded whorls are weaker, those of the sixth whorl do not reach the ventral side, hence the ventral side [umbilical zone] (fig. c) is smooth before the aperture; about 1/3 the distance beyond the peristome, five ribs

extend from the umbilicus nearly fusing together with some obliquely oncoming ribs from the upper part of the whorl as shown in Fig. 5C. The peristome is flatly bent back, the palatal lip is dented, the left columellar side sinks straight down, flattening at the rounded basal part of the aperture. Aperture shaped like a gourd. The ridge-like denticle nearest the columella [columellaris] reaches to the leftmost side of the parietal shield; the second, shorter ridge-like denticle [parietalis] extends from the parietal side and lies directly across from the shouldered edge of the right apertural lip. Height 2 1/8 mm, Width 1 1/3 mm.

Measurements. (BOKU F3444 from "Grotte hinter Laak", Slovenia): sh = 2.14 mm; sw = 1.09 mm; ah = 0.86 mm; aw = 0.67 mm; hlw = 1.17 mm; SA = 59.08 deg.

Distribution. (Hauffen *Z. costatum*) Cave behind Laak, Slovenia.

Enhanced description of *Z. costatum* based on integrative taxonomic analyses of Inäbnit et al. (2019) and Micro-CT and SEM Data in this work.

Diagnosis. Shell ca. 2 mm, transparent, ribbed, with weak spiral lines, elongate-conical with an auriform and more or less thickened peristome, bearing four apertural barriers, two of which continue on the columella as lamellae.

Description. Shell conical, translucent when fresh; whorls somewhat shouldered, usually stronger than in *Z. spelaeum*; pronounced, equidistantly-spaced axial ribs present on each whorl, though not always covering an entire whorl; weak spiral striae are usually visible; aperture taller than wide, the upper half of the palatal rim shouldered and expanded; the parietal shield well differentiated from lip, its margin more curved than straight; parietalis well developed in the aperture, extending one whorl into the shell; columellaris visible in aperture, extending 3⁄4 of a whorl into the shell; palatalis always present; angularis sometimes present. Internally, the base of the columella continually widens from below the point of attachment of the short, oblique lamella, forming a robust base above the umbilicus (Fig. 5E). The low columellaris increases structural form as it swells up towards the base of the columella (aperture facing right) (Fig. 5G), reaching its fullest size at half-way its distance on the columella (dorsal perspective) (Fig. 5F). Visible also in NHMW-MOL-71847 from Babja luknja, Goričane (fig. 5c1–3) (Inäbnit et al. 2019).

The *Z. costatum* shells (BOKU F3444a and BOKU 3473a) show the same lamella to columellar configuration as that seen in NHMW-MOL-71847 (Inäbnit et al. 2019) as well as the mode and degree of smoothness versus interconnected ribbing described by Freyer (1855) on the body whorl and the ventral side (Fig. 5J–K, M).

Considering the 10 specimens investigated in Inäbnit et al. (2019) and the two individuals in this study, *Z. costatum* differs from *Z. spelaeum* by the generally more expanded shoulder of the upper palatal rim (not visible in the broken shell of BOKU 3473a from Glaven vrh) and the swollen, wider basal configuration of the columella; differs from *Z. lamellatum* by its smaller, single lamella and reduced dentition; differs from *Z. lautum* by the marked presence of ribs and presence of a single lamella; differs from *Z. trebicianum* by its enhanced degree of ribbing and larger size.

Discussion

Conchological differences of considered morphological characters including fine or course ribbing, development or absence of spiral lines or the presence of a second parietalis, have long confounded taxonomists of the radially ribbed, zospeid morphs found in Dinaride caves and which were later lumped together under *Zospeum spelaeum schmidtii* (Frauenfeld, 1854) (Bole 1974). Later studies, based on comparative anatomical investigations (De Mattia 2005) and DNA sequence data (Inäbnit et al. 2019), rejected the subspecific dichotomy for *Zospeum spelaeum* (Rossmaessler 1839) in which the two species, *Carychium bidentatum* Hauffen 1856 and *Carychium reticulatum* var. *bidentatum* Hauffen 1856 became shuffled. All the while, type material of the two species could not be studied because it was considered lost until now. Though topotypic specimens of both species (Kuščer coll. Nrs. 437 and 10137 respectively) are known in the Ljudevit Kuščer collection in Trieste (MCSNTS) (De Mattia 2005), no other known *Zospeum* syntypes described by Heinrich Hauffen are preserved at the PMS, nor at the NHMW nor in the Freyer Collection housed at the MCSNTS (Inäbnit et al. 2019).

We remark that geographical names of towns and caves have changed through time via the historical reshuffling of geographical borders and languages such that there is no congruency, with today's names and those before WWII. Complicating the situation further, Hauffen tended to interchange annotation of locality names. For example, the type locality of *Z. reticulatum*, Bidou sturm, was recorded by Hauffen in 1856. In 1858, he refers to this locality as Bidov šturm at the Dobrus Mountain. Later, in 1932, the same cave locality was recorded by Kuščer as Bidov šturm (De Mattia, 2005). According to the Cave registry of the Speleological Association of Slovenia (Kataster JZS), the original name is considered Dobruška jama (sin. Jama nad Dobrušo) 46,175061, 14,476235; altitude 399 m a.s.l. (pers. com. Rajko Slapnik, June 2023). On the other hand, the type locality of *Z. bidentatum* was considered by Hauffen to be from a cave in a gorge at the Glavni verh near Habach castle (also: Schloss Habbach; Grad Jablje; Slovenia) in one publication (Hauffen 1858b). This locality is also recorded by Hauffen as Glavni verh in his earlier documentation (Hauffen, 1858a) and spelled differently (also: Glaven vrh, Glaven verh, Glavni vrh; meaning "main peak"; "Hauptgipfel" in German) on his labels accompanying the Bilimek Collection material here. According to the Cave registry of the Speleological Society of Slovenia (pers. com. Rajko Slapnik, Sept. 2023) and Bole (1974), the cave, Jama pod Sp. Dobenim is synonymous with Glaven verh, where the speleologists Kuščer, Bole, and Velkovrh are recorded to have collected *Zospeum* shells (Bole 1974). Kuščer (1932) mentions a small cave, with limited access, just below the village Dobeno near Mengs. Jože (1977) identifies Glaven verh as kind of a flooded cave below Ručigaj (in Spodnji Dobene near Mengš) (Fig. 6).

Hauffen's manuscript (Hauffen 1858b; Archiv NMS, leto 1856, št. 47) provides some further information about the characteristics of the small-scaled Glaven verh cave (Fig. 6), which should be located within a small canyon. The cave appears to be difficult to enter for ancient cavers (personal comm. Matija Križnar, 2024). The walls devoid of stalactites and the floor is covered with sand. A small stream should flow through the middle of the

cave. Ručigaj corresponds to Ručigajev izvir, while "izvir" can be translated as "spring". LiDAR (Light Detection and Ranging) photos confirm its position within a canyon.

Hauffen (1856a) loosely includes mention of the "Grottenschnecken" (= "cave snails"), *Carychium lautum* in "Glaven verh" and *Z. alpestre* (Freyer, 1855) in "Douga jama", which he also noted for harbouring *C. reticulatum* var. *bidentatum* in the same

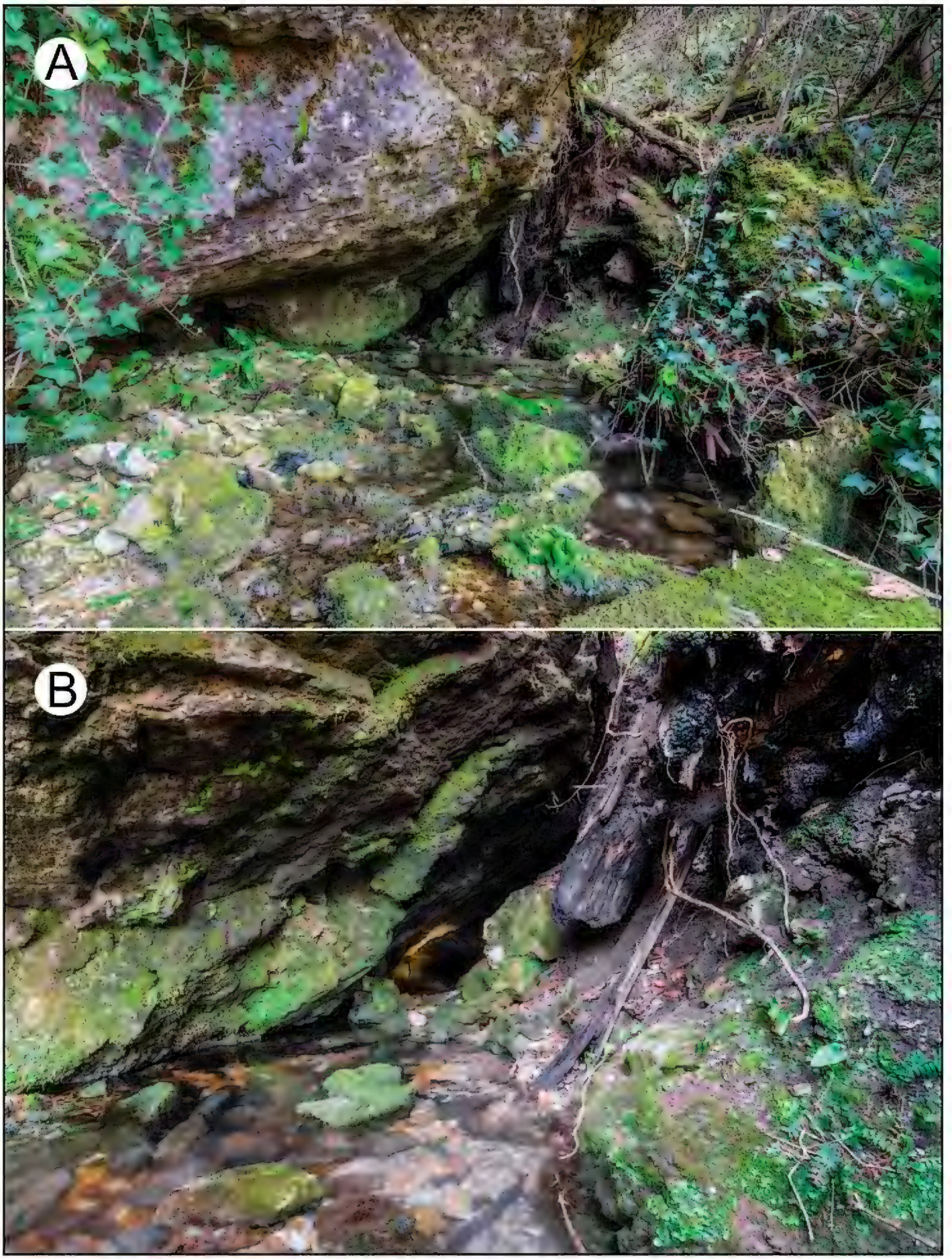

Figure 6. The narrow entrance of Glaven verh identified as Ručigaj = Ručigajev izvir, is located in a small canyon as described by Hauffen (1858b). Photos: Matija Križnar, 2024.

publication. Nevertheless, it is not clear if he actually sent this specific material, as stated therein to Frauenfeld, nor, if he later designated this material differently in his or another collection. We assume his notation referring to Glaven vrh all means the same cave by the Habach Castle (also known by 4 variable names, including Jablje Castle in Slovenian). Notable here, is that Inäbnit et al (2019) documents 3 shells (fig. 5d, NMBE 553383) from the nearby cave Jama 2 pri Jabljah (GPS: 46°08'30.9"N, 14°33'12.6"E) near Loka pri Mengšu (Laak bei Mannsburg). According to the Cave Registry of the Speleological Association of Slovenia, there is a very high density of caves within a very small radius in the region of Loka pri Mengšu of which Glaven verh (Ručigaj = Ručigajev izvir) is one.

By comparing our data to that of congeners in recent works (Inäbnit et al. 2019; Jochum et al. 2024), we reveal that the columellar apparatus of Hauffen's broken syntype of *C. reticulatum* from Glaven verh and the syntypes from "Grotte hinter Laak" (Hauffen 1856b) match well with that of *Zospeum costatum* (Freyer, 1855) in Inäbnit et al. (2019) (fig. 5c1–3). On the other hand, the columellar apparatus, aperture shape, whorl and spire formation and the umbilical configuration of Hauffen's *C. reticulatum* shells from Douga jama unequivocally match those within the spectrum of the species, *Z. spelaeum* (Rossmaessler 1839) in Inäbnit et al. (2019) (fig. 4b1–6). We emphasize that contemporary tools such as 3D X-ray Micro-CT and SEM imaging profoundly aid in the re-interpretation of former species designations while underscoring the significance of past evaluations in taxonomic investigations today.

The taxonomic examinations in this study therefore show that Hauffen's syntypes correspond morphologically to those of known species namely, *Zospeum spelaeum* (BOKU F3434b and BOKU F3429) and *Zospeum costatum* (BOKU F3444 and 3473a). By comparing key zospeid diagnostic characters beyond size, surface structure and dentition, additional ones, such as internal coiling configuration of the columellar apparatus, lamella formation in relation to the columella, the degree and size of the umbilical depression in conjunction with the formation of the final coiling in the umbilical zone (ventral perspective) (Jochum et al. 2024), this work underscores the considerations of previous taxonomists, Frauenfeld (1856), Freyer (1855) and Bole (1974) (i.e. *Z. spelaeum schmidtii*) in its current taxonomic placement within the *Z. spelaeum* clade in Inäbnit et al. (2019).

Conclusions

This work documents *Zospeum* syntypes considered lost to science from the original collection of Heinrich Hauffen and which later landed in the Dominik Bilimek collection at the BOKU in Vienna, Austria. The absence of reliable type material precluded their fullest consideration in the documentation and interpretation of *Z. costatum* (Freyer, 1855) and *Z. spelaeum* (Rossmaessler, 1839) in the most recent integrative taxonomic examinations of the genus *Zospeum* (Inäbnit et al. 2019). Our contemporary morphological analysis of *C. reticulatum* using light microscopy, SEM and X-ray Micro-CT data in conjunction with Hauffen's original documents and figures, illustrates the manifestation and degree of phenotypic variation on the shells (BOKU F3434b and BOKU F3429) of two populations of *Zospeum spelaeum*. Though we know little about the ecology of the

respective caves, cave systems in the region of Loka pri Mengšu are densely represented, with many being contiguous and thus, sharing subterranean drainage systems. *Zospeum* snails get washed through these systems during seasonal water flows and displacement of fauna within a concentrated system of caves is not unusual (Culver and Pipan 2009). Considering that *Z. s. schmidtii* was reported from many caves in the region and in several cases sympatrically with *Z. costatum* (Bole, 1974), the potentiality of mixing of populations is high. Reticulated microstructure of the teleoconch is also known in other species such as *Z. frauenfeldii* (Freyer, 1855) and *Z. costatum* (Freyer, 1855). We confirm that although the reticulated microstructure of Hauffen's specimens of *C. reticulatum* is more pronounced than in most other forms of *Z. spelaeum* of which it is considered a junior synonym, the shells (BOKU F3434b and BOKU F3429), and those of other former congeners such as the more or less reticulated variant, *Z. s. schmidtii* (see Bole 1974; Inäbnit et al. 2019), are otherwise, not differentiated enough to assign species status based on this character alone. We confirm that *C. reticulatum* Hauffen 1856 lies within the spectrum of character states taxonomically recognized for the species *Z. spelaeum* (Inäbnit et al. 2019). However, we remark that although this study considers the reticulated shells from the caves Bidou šturm and Douga jama to represent a phenotypic variation within the morphological spectrum known for *Z. spelaeum*, DNA sequence data from new material collected in these caves (and those of geographically proximal caves), would ultimately further our understanding of the *Z. spelaeum* clade. Since we do not rule out the potentiality that Hauffen's *C. reticulatum* populations might represent genetically separated evolutionary lineages of *Z. spelaeum* (i.e. having distinct DNA barcodes and nuclear DNA) (Weigand et al. 2014), this work especially opens new perspectives for future exploration and molecular investigations. Hence, we strongly encourage further speleological exploration and specimen collection in Bidou šturm (= Dobruška jama) as well as in Hauffen's listed cave localities (Table 1). Lastly, we emphasize that this study demonstrates the long-term scientific value and significance of the preservation and maintenance of historical, natural science collections.

Acknowledgements

We gratefully acknowledge the following contributions: Father Meinrad Tomann and Father Alkuin Schachenmayr (both Heiligenkreuz) for supporting this work with historical material from the archive; Gabriela Gelovizza (Trieste) for sending a high-resolution scan of a Bilimek photograph; Jürgen Kriwet (Vienna) for providing infrastructure for photography at the Department of Palaeontology (Vienna); Jan Steger (Vienna) for support with Scanning Electron Microscopy (SEM); Matija Križnar (Ljubljana) for photos and information on the Glaven vrh cave; Alexander Lukeneder (Vienna) is thanked for support with photography at the NHMW; Rajko Slapnik for his help in providing details from the Cave registry of the Speleological Association of Slovenia (Kataster JZS).

We thank the editor Alexander Weigand and two anonymous reviewers for their helpful comments and suggestions. Many thanks go to the Austrian Academy of Sciences (ÖAW) for financial support of this project. AJ received support from the SYN-

THESYS Project (financed by the European Community Research Infrastructure Action under the FP7 "Capacities" Program; project grant AT-TAF-5370). Open access funding provided by University of Vienna.

References

Albano PG, De Mattia W (2010) Rediscovery of the holotype of *Pterocera kochii* Freyer, 1855 (Gastropoda: Strombidae). Journal of Conchology 40(2): 163–167.

Bole J (1974) Rod *Zospeum* Bourguignat 1856 (Gastropoda, Ellobiidae) v Jugoslawiji. Razprave Slovenska Academija znanosti in Umetnosti, Cl. IV 17(5): 249–291.

Bourguignat JR (1856) Aménités Malacologiques. § LI. Du genre *Zospeum*. Revue et Magasin de Zoologie pure et appliquée [2] 8: 499–516.

Culver DC, Pipan T (2009) Biology of Caves and Other Subterranean Habitats. Oxford, U.K., Oxford University Press. https://doi.org/10.1093/oso/9780198820765.001.0001

De Mattia W (2003) Hypogean Molluscs of the Karst of Trieste (Italy). Atti del Museo Civico di Storia Naturale di Trieste 50: 89–218.

De Mattia W (2005) Slovenian hypogean molluscs (Prosobranchia: Hydrobiidae: Pulmonata: Ellobiidae) from Ljudevit Kuščer's collection kept in the Natural History Museum of Trieste (Italy). Malakologische Abhandlungen 23: 55–66.

Frauenfeld Von G (1854) Über einen bisher verkannten Laufkäfer beschrieben von L. Miller; und einen neuen augenlosen Rüsselkäfer, beschrieben von F. Schmidt; ferner einige von Schmidt in Schischka neu entdeckte Höhlentiere. Verhandlungen des Zoologisch-Botanischen Vereins in Wien 4: 23–34.

Frauenfeld Von G (1856) Die Gattung *Carychium*. Sitzungsberichte der mathematisch-naturwissenschaftlichen Classe der kaiserlichen Akademie der Wissenschaften 19: 70–93.

Frauenfeld Von G (1860) Sitzung am 7. November 1860. Verhandlungen der kaiserlich-königlichen zoologisch-botanischen Gesellschaft in Wien 10: 86.

Freyer H (1855) Über neu entdeckte Conchylien aus den Geschlechtern *Carychium* und *Pterocera*. Sitzungsberichte der Mathematisch naturwissenschaftlichen Classe der kaiserlichen Akademie der Wissenschaften, Wien 15: 18–23.

Hauffen H (1856a) Ueber ein neues *Carychium*. Verhandlungen des Zoologisch-Botanischen Vereins in Wien 6: 623–624.

Hauffen H (1856b) Zwei neue Schnecken. Verhandlungen des Zoologisch-Botanischen Vereins in Wien 6: 701–702.

Hauffen H (1858a) Systematisches Verzeichnis der Land- und Süßwasser-Conchylien Krain's. Separat-Abdruck aus dem Jahreshefte des Vereins des krainischen Landes-Museums, Laibach, 38 pp.

Hauffen H (1858b) Beiträge zur Grottenkunde Krains. Zweites Jahresheft des Vereines des krainischen Landes-Museums, Laibach: 40–53.

Hopfensperger B, Maletz J, Lukeneder P, Heinz P, Ottner F (2021) Early graptolite research: Eduard Suess and the Bilimek collection. Bulletin of Geosciences 96(3): 279–293. https://doi.org/10.3140/bull.geosci.1829

Inäbnit T, Jochum A, Kampschulte M, Martels G, Ruthensteiner B, Slapnik R, Nesselhauf C, Neubert E (2019) An integrative taxonomic study reveals carychiid microsnails of the troglobitic ge-

nus *Zospeum* in the Eastern and Dinaric Alps (Gastropoda, Ellobioidea, Carychiinae). Organisms Diversity & Evolution 19(2): 135–177. https://doi.org/10.1007/s13127-019-00400-8

International Commission on Zoological Nomenclature. (1999) International Code of Zoological Nomenclature. (4th edn.). London, U.K. [available online at http://www.iczn.org/iczn/index.jsp]: International Trust for Zoological Nomenclature.

Janssen R (2006) Adolf Zilch. Archiv für Molluskenkunde 135(1): 1–21. https://doi.org/10.1127/arch.moll/0003-9284/135/001-021

Jochum A, Michalik P, Inäbnit T, Kneubühler J, Slapnik R, Vrabec M, Schilthuizen M, Ruthensteiner B (2024) 3D X-ray microscopy (Micro-CT) and SEM reveal *Zospeum troglobalcanicum* Absolon, 1916 and allied species from the Western Balkans (Ellobioidea: Carychiidae). European Journal of Taxonomy 926: 1–62. https://doi.org/10.5852/ejt.2024.926.2469

Jože, B (1977) Hypogean Snails in Isolated Karst of Posavje Mountains. Naše jame 18: 32–37.

Kuščer L (1932) Höhlen- und Quellenschnecken aus dem Flußgebiet der Ljubljanica. Archiv für Molluskenkunde 64: 48–62.

Lukeneder P, Liebhart, I, Ottner, F, Mikes, A, Heinz, P, Polách, R (2023) The historical power of the natural science collection of Dominik Bilimek at the University of Natural Resources and Life Sciences, Vienna (BOKU). Notes and Records. The Royal Society Journal of the History of Science. https://doi.org/10.1098/rsnr.2022.0051

Rossmaessler, EA (1839) Iconographie der Land- und Süsswasser-Mollusken, mit vorzüglicher Berücksichtigung der europäischen noch nicht abgebildeten Arten. 1: 2 (3/4) (p. 46). Dresden, Leipzig: Arnoldische Buchhandlung.

Roth HJ (1965) Dominik Bilimek Leben und Werk eines österreichischen Naturforschers. Sudhoffs Archiv für Geschichte der Medizin und der Naturwissenschaften 49(4): 338–354.

Roth HJ (2016) Der sterbende Kaiser und sein Naturforscher. Dominik Bilimek, Zisterzienser im Dienste des Kaisers Maximilian von México. 1. Folge. Magazin für Amerikanistik. Zeitschrift für amerikanische Geschichte 40(4): 17–21.

Roth HJ (2017) Der sterbende Kaiser und sein Naturforscher. Dominik Bilimek, Zisterzienser im Dienste des Kaisers Maximilian von México. 2. Folge. Magazin für Amerikanistik. Zeitschrift für amerikanische Geschichte 41(5): 39–43.

Salvador RB, Breure ASH, Hannam S, Blom WM (2023) South American terrestrial Gastropoda in the collection of the Auckland War Memorial Museum. Tuhinga 34: 57–73. https://doi.org/10.3897/tuhinga.34.98329

Schiner R (1854) Fauna der Adelsberger-, Lueger- und Magdalenen-Grotte. In: Schmidl A (Ed.) Die Grotten und Höhlen von Adelsberg, Lueg, Planina und Laas. Braumüller, Wien: 234–272.

Sturm J (1847) Deutschlands Fauna in Abbildungen nach der Natur mit Beschreibungen. Band 19. Nürnberg.

Weigand AM, Jochum A, Klussmann Kolb A (2014) DNA barcoding cleans house through the Carychiidae (Eupulmonata, Ellobioidea). American Malacological Bulletin 32(2): 236–245. https://doi.org/10.4003/006.032.0215

Wenzel W (1992) Bibliographie für Karst- und Höhlenkunde aus ÖTK-Schriften. 1. Teil. Wissenschaftliche Beihefte zur Zeitschrift „Die Höhle“ 41: 3–115.